

Variability in Osteon Size in Recent Human Populations

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ABSTRACT The possibility of smaller osteons in the cortical bone of Late Pleistocene human populations begs the question of how these histological features vary within individual skeletons among and between populations. The distributional characteristics of total osteon area (On.Ar) and Haversian canal area (H.Ar) are explored using data from three samples of historically known individuals: ribs and femora from eighteenth-century Huguenots in England (Spitalfields, $n = 20$), ribs and femora from nineteenth-century British settlers in Canada (St. Thomas, $n = 21$), and ribs from twentieth-century South African cadavers (University of Cape Town; following curatorial classifications, $n = 10$ white, 10 black, 10 colored). Neither histological variable is normally distributed. About 96% of the random variation is within the individual bone sample. There are no significant differences between sexes for either variable in any sample, and age has no effect in most instances. Femoral osteons are significantly larger than rib osteons within individuals and across samples. Haversian canal area is more variable than On.Ar, especially in the twentieth-century sample, where within-sample coefficients of variation are frequently $>100\%$. Using modern centiles developed here, some Late Pleistocene long bone samples have On.Ar values below the range of modern variation. Because of ribs' smaller cross-sectional areas and less broadly ranging values for On.Ar, ribs would provide a preferable site for future comparative studies. *Am J Phys Anthropol* 106:219-227, 1998.

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Anthropologically oriented study of human bone at the tissue level is conceptually attractive. Through it we should be able to learn about the life characteristics of deceased individuals, similar to the sort of information that can be obtained from bone histomorphometry in modern clinical medicine (Weinstein, 1992; Parfitt, 1992). Recent publications by Abbott et al. (1996) and Pfeiffer and Zehr (1996) note that cortical bone from Late Pleistocene humans appears to show smaller osteons than bone from modern humans. However, this observation must necessarily be tentative because it is based on our limited knowledge of how these structures vary within human skeletons and between modern human populations. Inter-

est in using osteon population density for estimating age at death has lead to observations on the variability of osteon organization throughout cortical bone (Pfeiffer, 1992; Lazenby and Pfeiffer, 1993; Stout and Gehlert, 1979; Pfeiffer et al., 1995; Stout and Stanley, 1991), but relatively little has been published describing cortical osteon size (Evans, 1976a,b; Stout, 1976; Stout and Teitelbaum, 1976). Future research on ancient bone tissue would benefit from a stron-

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ger base of information about modern humans. The histomorphometric literature is of little use because its emphasis is on cancellous bone tissue and the analytical site of choice is the iliac crest, a sampling site that is rarely used in anthropological studies.

This study focuses on two variables which have been noted in both the anthropological and clinical literature and which together represent the resorption and depositional parameters of cortical remodeling events. The extent to which the bone remodeling unit (BRU) resorbs the preexisting cortical bone will determine the location of the reversal line and hence the area of the osteon. The extent to which the subsequent refilling of that resorption space is completed by the BRU will determine the area of the Haversian canal (Eriksen et al., 1994). These two variables form the bases for calculating other histomorphometric variables such as wall thickness. The purpose of this study is to quantify the variability of these structures in a diverse array of recent human samples and to determine the extent to which that diversity can be apportioned to the fundamental variables of sex, age, and population/environment. Once the modern range for these two variables is established, the previously published values for Late Pleistocene *Homo* can be compared to that range.

MATERIALS

The eighteenth-century Huguenot ribs and femora are from a subset of the very large sample of skeletons excavated from the crypt at Spitalfields, London, England (Molleson and Cox, 1993). All are named individuals with known ages at death. In an attempt to maximize relevance to the study of prehistoric human populations, relatively young adults were chosen. There are nine females (ages 26–37 years) and 11 males (ages 25–50 years), each represented by rib and femur sections. Years of death range from AD 1756–1835. Tissue samples were retained in anticipation of the materials' reinterment.

The nineteenth-century Canadian settler ribs and femora are from a subset of the very large sample of skeletons excavated at St. Thomas Anglican Church, Belleville, Ontario (Saunders et al., 1995; Herring and Saunders, 1992). All are named individuals

with known ages at death. There are seven females (ages 17–67 years) and 14 males (ages 20–81 years), each represented by rib and femur sections. Years of death range from AD 1827–1873, with most being in the 1860s. Tissue samples were retained prior to the materials' reinterment.

The twentieth-century ribs are from cadavers of the Anatomy and Cell Biology Department at the University of Cape Town (UCT), representing deaths from 1984–1991 (Pratte and Pfeiffer, 1996). All are named individuals, although age at death may have been unofficially documented for some individuals and hence less certain than ages based on birth certificates. Following the official system of categorization in place at the time of autopsy, the sample includes ten blacks (ages 24–88 years), ten whites (ages 49–95 years), and ten coloreds (ages 32–74 years), each equally represented by males and females. While the biological meaning of these categories may be unclear, this sample taken collectively represents substantial genetic heterogeneity. Unlike the Spitalfields and St. Thomas samples, the UCT cadavers are a permanently curated resource. The rib samples could be removed with minimal disturbance, since the rib cage had been cut at autopsy. Permission was not requested to remove tissue from the femora.

METHODS

All femoral sections are transverse samples from the midshaft, right femur preferred. The linea aspera region is not included within the Spitalfields samples, which are anteriorly oriented, c-shaped sections. To maintain consistency, the linea aspera region was not included when measuring osteons in St. Thomas femora either. The rib tissue was sampled from the sixth rib in the St. Thomas and Cape Town samples and from an unspecified mid-thoracic rib in the Spitalfields sample. All ribs were sampled at a location about one-third along the length of the rib, viewed from the sternal end. In the Cape Town samples, this was the exposed portion following the removal of the breast plate at autopsy. Ribs showing fracture healing or other obvious pathological changes were avoided.

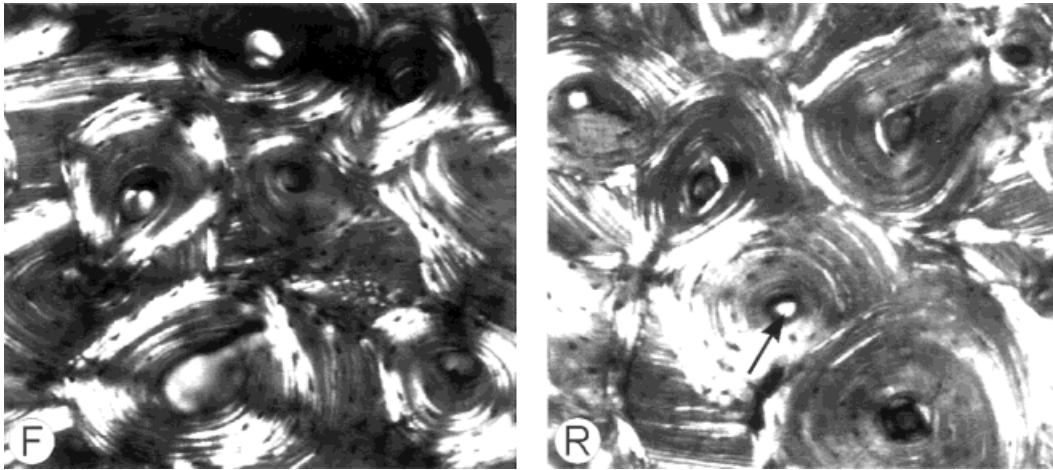


Fig. 1. Optimas images, like those used in this study, from the cortex of the femur (F) and rib (R) of a 34-year-old man from the Spitalfields sample at identical levels of magnification. While osteon areas appear roughly equivalent in these images, the Haversian canals (as per arrow) are notably smaller in the rib.

Approximately 50 osteons were measured per thin section. To avoid confounding this study of osteon size with the matter of variability in osteon shape, an osteon was measured only if its greatest diameter was no more than twice its smallest diameter and its outer reversal line was complete. Thus, there was a bias toward circular structures and an avoidance of structures that were cut obliquely in sample preparation. An attempt was made to sample osteons from throughout each thin section, including the periosteal, mid-cortex, and endosteal bone envelopes. However, since many endosteally positioned osteons are irregular in shape, this region may not be represented as frequently. This will tend to reduce the mean size of osteons, since endosteally positioned structures tend to be larger. Physical preservation of the tissue is variable, such that diagenesis also sometimes influenced the sampling but in a random fashion.

All cortical bone samples were prepared as undecalcified thin sections and were examined under polarized light with a Nikon Labophot binocular microscope. The images were conveyed via a video camera mounted on the microscope to a computer equipped with Bioscan Optimas 4.02 software (Fig. 1). Calibration was established using a stage micrometer and was reconfirmed intermit-

tently throughout the data collection period. Variables collected include total osteon area (On.Ar) (the area circumscribed by the reversal line) and Haversian canal area (H.Ar), (the area circumscribed by the inner edge of the osteon bone tissue) (Parfitt et al., 1987). In total, 2,029 femur osteons and 3,365 rib osteons were measured. Intraobserver error, calculated from triplicate measurements taken over a period of 2 months, averaged 3.7% (Dupras, 1995). Statistical analyses are based on factorial nested ANOVA with unequal numbers of replicates, incorporating a split plot design for the rib-femur comparisons.

RESULTS

Summary statistics for all samples are presented in Figures 2 and 3 and Tables 1 and 2. Distributions for both femoral and rib On.Ar are leptokurtotic with modal values below the mean and rightward skewness. Distributions of both femoral and rib H.Ar are even more leptokurtotic and rightwardly skewed, but modal values are very close to the mean. Data were transformed using $(\log + 3500)$, such that On.Ar values are normally distributed. This transformation improved the distributional characteristics of H.Ar, but these data remain nonnormal.

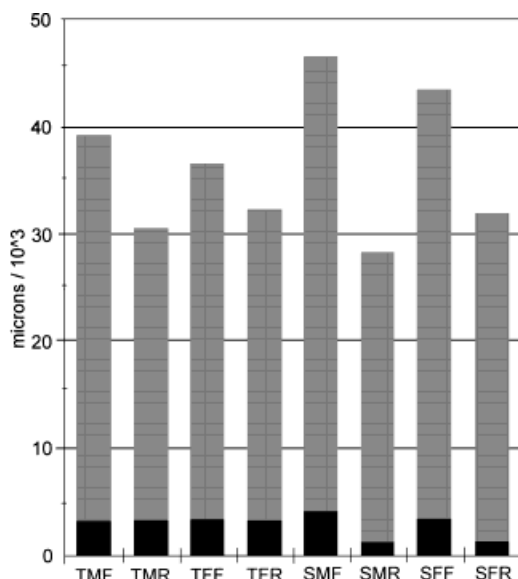


Fig. 2. Graphic representation of osteon areas from St. Thomas (T) and Spitalfields (S) males (M) and females (F), femora (F) and ribs (R); e.g., TMF, St. Thomas male femora. More deeply shaded portion = H.Ar.

Covariance parameter estimates indicate that a very small amount of the random variance can be attributed to demographic characteristics of the individual, about 4% for both On.Ar and H.Ar. Fixed effects ANOVA demonstrated no age effects, so subsequent analyses focused on sex and sample effects. Variation within H.Ar is consistently greater than that within On.Ar. Coefficient of variation values for H.Ar are frequently above 100%, values that are twice to three times as high as the values for On.Ar.

Comparison of ribs with femora

Both overall ($f = 86.85$, $P < 0.01$) and in the Spitalfields and St. Thomas samples considered separately, osteon areas from ribs are significantly smaller than osteon areas from femora (35 df, Spitalfields $t = 8.24$, $P < 0.01$; St. Thomas $t = 4.90$, $P < 0.01$) (Fig. 1). There is a significant site effect ($f = 5.63$, $P < 0.05$) and an interaction between bone and sample (35 df, $f = 6.18$, $P < 0.02$), reflecting the lesser magnitude of difference in the St. Thomas sample. Within individuals, this relationship holds in 38 of 40 pairs. Only two females, both from St.

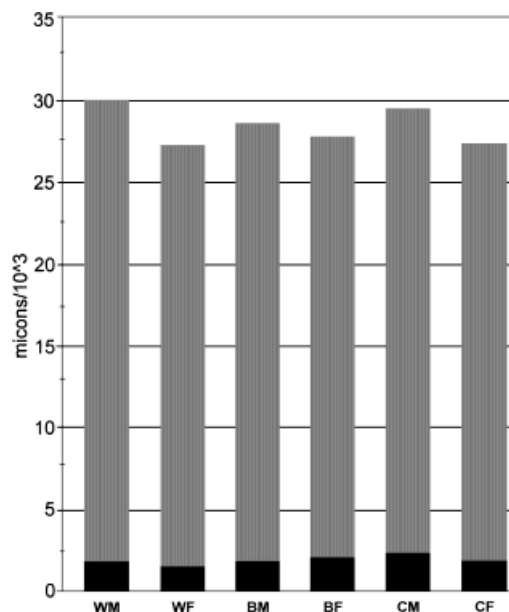


Fig. 3. Graphic representation of osteon areas from the Cape Town cadaveral sample divided by historically designated group. Legend and mean age of each subset: WM, white males, 63.8 years; WF, white females, 79.6 years; BM, black males, 59.8 years; BF, black females, 46.4 years; CM, colored males, 48.3 years; CF, colored females, 66.3 years. More deeply shaded portion = H.Ar.

Thomas, have larger rib On.Ar. The size difference in these two cases is small, about $500 \mu\text{m}^2$. Haversian canal areas are significantly different overall ($f = 71.03$, $P < 0.01$) and in the Spitalfields sample ($t = 12.49$, $P < 0.01$) but not in the St. Thomas sample ($t = 0.73$). Here again there is a significant site effect ($f = 30.14$, $P < 0.01$) and interaction between bone and sample ($f = 89.23$, $P < 0.01$). No comparisons based on sex show statistical significance.

In the Spitalfields sample, the magnitude of the difference in osteon area is about the same in both sexes, with rib On.Ar being 66% that of femur On.Ar in males and 73% that of femur On.Ar in females. These values for the St. Thomas sample are 78% for males and 91% for females. In both samples there is less difference in magnitude among the females. Neither variable shows a significant sex interaction effect.

Variability among femora

Comparing the two samples, mean values for On.Ar show about a $10,000 \mu\text{m}^2$ spread.

TABLE 1. Summary of histological measurements of femora and ribs, all samples¹

	On.Ar			H.Ar		
	MEAN	S.D.	C.V.	MEAN	S.D.	C.V.
Femora: Spitalfields	45,040.1	23,541.4	52.3	3,835.1	4,676.5	121.9
Males (N = 550, n = 11)	46,460.3	24,991.9	53.8	4,119.4	5,241.9	127.2
Females (N = 400, n = 9)	43,087.4	21,263.0	49.3	3,444.3	3,734.3	108.4
Femora: St. Thomas	38,059.9	18,068.6	47.4	3,176.9	1,905.1	60.0
Males (N = 737, n = 14)	39,157.8	18,874.4	48.2	3,156.6	1,827.3	57.9
Females (N = 342, n = 7)	35,694.0	15,967.4	44.7	3,220.7	2,064.9	64.1
All femora	41,328.1	21,095.3	51.0	3,485.1	3,503.0	100.5
Ribs: Spitalfields	31,142.0	12,621.5	40.5	1,376.9	878.7	63.8
Males (N = 452, n = 10)	30,789.8	11,925.9	38.7	1,416.0	933.2	65.9
Females (N = 357, n = 9)	31,587.8	13,454.5	42.6	1,327.4	802.9	60.5
Ribs: St. Thomas	31,257.5	15,743.0	50.4	3,373.7	2,049.9	60.8
Males (N = 701, n = 14)	30,714.9	15,269.9	49.7	3,431.8	2,077.3	60.5
Females (N = 355, n = 7)	32,329.0	16,607.8	51.4	3,258.9	1,992.7	61.1
Ribs: Cape Town	28,441.5	16,606.1	58.4	1,885.6	3,119.0	165.4
Males (N = 800, n = 16)	28,916.3	17,367.7	60.1	1,897.7	3,173.5	167.2
White (N = 250, n = 5)	30,000.3	17,801.7	59.3	1,788.5	3,115.2	174.2
Black (N = 250, n = 5)	27,220.0	16,742.2	61.5	1,451.1	1,692.3	116.6
Colored (N = 300, n = 6)	29,426.5	17,466.1	59.4	2,360.9	4,006.6	169.7
Females (N = 700, n = 14)	27,898.9	15,685.3	56.2	1,871.7	3,057.8	163.4
White (N = 250, n = 5)	28,548.9	15,197.7	53.2	1,768.0	2,024.1	114.5
Black (N = 250, n = 5)	27,726.1	17,263.5	62.3	2,075.4	4,451.2	214.5
Colored (N = 200, n = 4)	27,302.5	14,189.9	52.0	1,746.7	1,696.2	97.1
All ribs	29,974.5	15,516.5	51.8	2,230.3	2,544.9	114.1

¹ All measurements are in μm^2 . H.Ar, Haversian canal area; N, number of osteons measured; n, number of humans sampled; On.Ar, osteon area. Subdivisions of Cape Town sample (black, white, colored) are based on the designations given the cadavers at acquisition, 1984–1991.

TABLE 2. Centiles, based on weighted averages, for histological variables¹

	Fifth	Tenth	Twenty-fifth	Fiftieth	Seventy-fifth	Ninetieth	Ninety-fifth
Femur							
On.Ar	16,479.6	19,883.6	26,773.7	36,903.3	51,494.7	67,580.8	80,273.4
H.Ar	956.1	1,177.2	1,745.5	2,633.5	4,123.5	6,193.0	8,350.7
Rib							
On.Ar	10,558.6	13,137.2	18,916.1	27,201.0	37,755.9	49,913.7	58,346.2
H.Ar	472.0	595.1	924.5	1,510.5	2,735.4	4,480.1	5,875.4

¹ Based on 2,029 femur osteons and 3,365 rib osteons. All values are in μm^2 . H.Ar, Haversian canal area; On.Ar, osteon area.

Although in both samples female On.Ar values are lower than male values, these differences are not statistically significant. Haversian canal areas are not significantly different between sexes within samples.

Among the Spitalfields femora, there are significant positive correlations between On.Ar and age ($R^2 = 0.62$) and H.Ar and age ($R^2 = 0.66$). For On.Ar, the correlation is strongly influenced by the two eldest individuals, both males, who have large osteons and large Haversian canals. When they are removed, the On.Ar correlation becomes non-significant. However, for H.Ar, the strength of the relationship diminishes but remains significant when these two cases are removed ($R^2 = 0.46$). Within the St. Thomas sample, there are no statistically significant

relationships between the osteon measurements and age at death.

Variability among ribs

For both On.Ar and H.Ar, the ANOVA analysis of fixed effects demonstrates a significant sample effect but not a sex effect. Comparing the samples, mean values for On.Ar show about a 4,000 μm^2 spread, from the Spitalfields females at 31,587 to the Cape Town black males at 27,220. Relative to the magnitude of the overall mean, this is about half as broad a range as shown by On.Ar in the femur. Both the Spitalfields and St. Thomas female rib samples show absolutely but nonsignificantly larger On.Ar than in those of males. In the Cape Town sample, males show absolutely but nonsig-

nificantly larger On.Ar than females. This pattern holds for all subsets of the Cape Town sample: blacks, whites, and coloreds (Fig. 3). There are no significant differences between subsets of the Cape Town sample for any variable. Comparing On.Ar values, both Spitalfields and St. Thomas show significantly larger values than Cape Town blacks ($t = 3.76$, $P < 0.01$; $t = 3.25$, $P < 0.02$, respectively). Spitalfields shows values for H.Ar that are significantly smaller than those of St. Thomas ($t = 12.29$, $P < 0.01$). St. Thomas shows values for H.Ar that are significantly larger than those from Cape Town whites, blacks, and coloreds ($t = 9.32$, 9.50 , and 7.75 , respectively, all $P < 0.01$).

Within the St. Thomas and Cape Town samples, there are no statistically significant relationships between the osteon measurements and age at death. An expanded sample of ribs from Spitalfields adults aged 20–50 years ($n = 58$) showed a significant increase in H.Ar among females (Dupras, 1995) but no other relationships with age.

Comparison with published values

Because previously published values are not always clearly defined or accompanied by error terms, statistical comparisons cannot be made. The mean value for femoral On.Ar reported here ($41,328 \mu\text{m}^2$) is similar to the values for males ($35,288.9 \mu\text{m}^2$) and females ($41,046.6 \mu\text{m}^2$) from Pecos Pueblo published by Abbott et al. (1996), except that the Pecos Pueblo values show the female value to be larger than the male value. The On.Ar values for the ribs studied here are of course comparable to those from an expanded sample of Spitalfields ribs published earlier, although among those 58 samples males show On.Ar values which are 96% the size of females (Dupras and Pfeiffer, 1996).

The centile values for On.Ar and H.Ar based on the complete set of measured osteons are shown in Table 2. While they represent only the femur and the rib, it may be useful to compare all available Late Pleistocene data, including specimens from the tibia and humerus, for purposes of hypothesis formulation. The On.Ar values for late Pleistocene *H. sapiens* (Abbott et al., 1996) frequently fall below the fiftieth centile of modern values. Only the Shanidar 2 tibia

and the Skhül 6 femur fall between the fiftieth and seventy-fifth centiles. Femoral values for Tabun, Shanidar 4, and Broken Hill fall between fiftieth and twenty-fifth centiles; Skhül 7, Shanidar 5, and Shanidar 6 fall between twenty-fifth and tenth, Shanidar 3 falls between tenth and fifth, and Skhül 3 falls below the fifth. Values for the Border Cave humerus (Pfeiffer and Zehr, 1996) fall between twenty-fifth and tenth femoral centiles or between fiftieth and twenty-fifth rib centiles. Therefore, there does appear to be a strong trend toward smaller osteons in the Late Pleistocene.

DISCUSSION AND CONCLUSIONS

Osteon areas within a single section of cortical bone are highly variable. Using rib data, a power test (Sokal and Rohlf, 1969) suggests that if a difference in size of 25% exists between two samples, it would take measurements of 68 osteons per sample to confirm this difference at the $P = 0.05$ level. Values presented here, based on 50 osteons per bone section, will be sufficient only to differentiate samples that are very different. Haversian canal sizes within an individual sample are much more variable than osteon sizes, so it is possible that biologically meaningful patterns of size difference will be very difficult to discern. Alternately, comparisons of sample statistics in a fashion in which the variability within each individual is masked—for example, using a single mean value per person—may yield falsely significant differences.

The samples included in this study show no significant patterns of relationship between histological variables and sex, and comparisons with previously published values suggest that the consistent but nonsignificant pattern seen here, of females showing lower values than males, occurs by chance. The samples in this study show different, generally nonsignificant patterns of relationship between histological variables and age. The Spitalfields sample shows some statistically significant changes with age, yet the St. Thomas and Cape Town samples do not. These weak or nonexistent relationships are consistent with a previous study of osteon size in the St. Thomas sample alone which demonstrated a lack of

statistical correlation between osteon area and age at death, femur length, total cross-sectional area, percent cortical area, or polar moment of area (Pfeiffer and Zehr, 1995).

It is intriguing that among the rib samples there are no significant differences among the most recent (Cape Town) samples, yet there are differences between the earliest (Spitalfields) group and the others. The Spitalfields sample shows the largest femoral osteons and the smallest rib Haversian canals. If the assertion is accepted that the Cape Town samples incorporate substantial genetic diversity, the results suggest that unidentified environmental factors are contributing more to the variance than genetic factors. This same argument can be mounted from the observation that among Late Pleistocene samples both "modern" and "neanderthal" specimens show low On.Ar values.

It is possible that with further descriptive work we may be able to use histological variables like On.Ar and H.Ar as benchmarks for population relationships and metabolic health, respectively. The variable nature of H.Ar is consistent with its link to bone remodeling and calcium metabolism. Partially filled osteons will have relatively larger Haversian canals, while fully filled osteons will have smaller ones. Perhaps the lower variability in the femurs and ribs of the nineteenth-century rural sample (St. Thomas) reflects a higher proportion of accidental deaths or briefer periods of pre-mortem ill health. The documented causes of death for the Cape Town sample are mainly diseases. These conditions may have been under treatment, possibly for prolonged duration. The nineteenth-century deaths represented in the St. Thomas sample may have occurred after a shorter period of morbidity. The intermediate coefficient of variation values for femur H.Ar in the eighteenth-century urban sample, Spitalfields, would reflect an intermediate length of morbidity prior to death. However, Spitalfields shows low variability for rib H.Ar. This, plus the small size of the Spitalfields rib Haversian canals, remains unexplained. The significant difference between H.Ar in ribs and femora in the Spitalfields sample seems inconsistent with the assumption that H.Ar reflects whole body metabolic activity.

Hypotheses for why differences in osteon area may exist for the same bone between human populations, such as those seen between Late Pleistocene and modern femora, may be based on a biomechanical rationale (Abbott et al., 1996) or on endocrine factors (Weinstein, 1992). The clinical histomorphometric literature demonstrates that histological structures will be influenced by a number of diseases and some lifetime behavioral choices (Kanis, 1995; Laitinen and Valimaki, 1991; Lindholm et al., 1991; Eriksen et al., 1994). Experimental biomechanical research demonstrates that changes to loading can also affect histological structures. There is clear evidence from comparative anatomy that there are species-specific patterns of bone histology. That is, there is a genetic predisposition to histological structures of particular shapes and sizes (Foote, 1916; Enlow and Brown, 1956, 1957, 1958).

The suggestion that the smaller osteons of late Pleistocene femora might reflect a response to greater biomechanical loading and a reduced rate of remodeling among these robust individuals is not supported by the present work, where ribs show consistently smaller osteons than femora. Experimental study demonstrates a higher remodeling rate in the rib as compared to the femur (Marotti, 1976), challenging the assertion that reduced formation will be linked to the formation of smaller osteons. Different fields of the human skeleton respond to growth stimuli in different ways, and so it could be argued that femora and ribs are differently canalized, leading to osteons of different sizes but similar coefficients of variation (Waddington, 1957; Tanner, 1978). Whether the difference seen here between rib and femur osteon areas is due to genetic factors, biomechanical factors, localized patterns of cartilage sensitivity to hormones, or a combination of these and other factors cannot be determined from this study. Future explanatory models for histological differences in human cortical bone should be broadly based in functional biology.

Given the narrower range of rib osteon area measurements across population samples and the rib's smaller cross-sectional area, it would be desirable if future studies focused on the rib as a sample location.

Given that the average adult rib cross-section includes approximately 150–300 osteons, some of which are irregular in cross-section and some of which are diagenetically obscured, 50 measured osteons (preferably more) will represent a large proportion of those that can be measured, practically speaking. Studies of femoral cross-sections, with their thousands of osteons, will be confounded by variability within the scantily sampled section and variability related to the exact location along the shaft. When sites other than the rib or femur must be used, the comparison should be with modern samples from that same bone using the same sampling location. High variability in osteon areas within a thin section necessitates the measurement of as many osteons per sample as possible.

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